

STUDY ON THE MORPHOLOGY OF FIVE MEDITERRANEAN
AND ATLANTIC SPARID FISHES WITH A REINSTATEMENT OF
THE GENUS *PAGRUS* CUVIER, 1817

by

G. BIANCHI (1)

ABSTRACT.— After Cuvier separated the genus *Pagrus* from *Sparus* on the basis of a different number of rows of molars in both jaws, some authors argued that this character, because of its variability, was not sufficient to separate the two genera. On this basis, *Pagrus* was recently synonymized under *Sparus*. The osteological and meristic differences found in the species under study (*Sparus aurata*, *Pagrus africanus*, *P. auriga*, *P. caeruleostictus*, and *P. pagrus*) suggest that the separation of these two genera should be maintained until the relationships among the various genera of the family will be better understood.

RESUME. — Cuvier sépara le genre *Pagrus* du genre *Sparus* d'après le nombre différent de rangées de molaires aux deux mâchoires ; cependant certains auteurs montrèrent que ce caractère, à cause de sa variabilité, n'était pas suffisant pour distinguer les deux genres. Pour cette raison, *Pagrus* a récemment été placé en synonymie de *Sparus*. Les différences ostéologiques et méristiques observées chez les espèces étudiées par l'auteur (*Sparus aurata*, *Pagrus africanus*, *P. auriga*, *P. caeruleostictus* et *P. pagrus*) suggèrent que la distinction de ces deux genres doit être maintenue jusqu'à ce que les relations entre les différents genres de la famille soient mieux comprises.

Key-words : Sparidae, *Pagrus*, *Sparus*, Morphometry, MED, AE.

INTRODUCTION

The purpose of this study is to clarify the relationships between five Mediterranean and Atlantic species attributed to the genus *Sparus* Linnaeus, 1758 by recent authors but formerly considered as belonging to two different genera, *Sparus* Linnaeus, 1758 and *Pagrus* Cuvier, 1816.

The genus *Sparus* was established by Linnaeus (type-species : *Sparus aurata* Linnaeus, 1758 and included 22 species from various parts of the world. With the recognition of many new species, the original Linnean genus was split into a number of well defined genera [Jordan and Fesler (1893), Regan (1913), Fowler (1933) and Smith (1938)].

Cuvier established the genus *Pagrus* in 1817 [type-species : *Sparus argenteus* Bloch and Schneider (1801) = *Sparus pagrus* Linnaeus, 1758] and distinguished it

(1) Marine Resources Service, Fishery Resources and Environment Division, Food and Agriculture Organization of the United Nations, Via delle Terme di Caracalla, 00100 Rome, Italy.
Cybio 1984, 8(4) : 31-56

from *Sparus* by the presence of two rows of molars instead of three or four.

Jordan and Fesler (1893) did not agree on this separation : « The species [of the genus *Sparus*] have been commonly distributed in two genera: *Pagrus* with the molar teeth in two series, and *Sparus* with the molars in three or more. This character has not much importance, and Steindachner has proposed to substitute for it the following :

Sparus : Teeth behind the canines, with the apex rounded, granulated, or globose; molars in two or more series.

Pagrus : Teeth behind the canines acute, subulate or setaceous; molars in two or more series.

Although in general appearance *Sparus aurata* and *Sparus pagrus* differ considerably, there is no important difference in the skull or skeleton, and we place all in one genus. »

Jordan and Thompson (1914) considered *Sparus* and *Pagrus* two separate genera since « all *Sparus* species are olive and silver in colour, never red and the teeth are in broader bands, the upper molars in three or more series ».

Smith (1938) in his key to the South African genera of the subfamily Sparinae included the Mediterranean-Eastern Atlantic genus *Sparus* for which he used the following distinguishing characters : « Anterior teeth conical; scales small, more than 70 series; all scales cycloid ». He clearly included in this genus only *Sparus aurata* since it is the only Mediterranean-Eastern Atlantic species having strong canines and molars and more than 70 lateral-line scales.

Munro (1949) suggested that since *Sparus aurata* Linnaeus, 1758 is the type-species for the genus *Sparus* and this species has characters that distinguish it from all other Sparidae, *Sparus* be considered a monotypic genus.

Akazaki (1962) treated *Pagrus* as a valid genus to be distinguished from *Sparus* by the following characters :

	<i>Pagrus</i>	<i>Sparus</i>
outer canines in upper jaw	4	6
outer canines in lower jaw	4 to 6	6
series of molars	2	more than 4 series
dorsal fin spines	XII	XI
dorsal fin rays	10 (11)	11 to 13
anal rays	8 or 9	11 (10)
scales on head	extending to inter-orbital region	not extending to interorbital region
body colour	pinkish or reddish	greyish silver or olive silver

Bini (1968) maintained the distinction between *Sparus* and *Pagrus* based on the different number of rows of molar teeth.

Tortonese (1970) in his book on the fishes found in Italian coastal waters, used the genus *Sparus* for all the species with strong canines anteriorly and two to four rows of molars laterally. He argued that the tooth character is not sufficient to se-

parate *Pagrus* from *Sparus* since the number of rows of molars changes with growth and does not clearly separate the two taxa. He united the two genera under the older name *Sparus*. He also maintained this position in the Check-list of the Fishes of the Northeastern Atlantic and of the Mediterranean (CLOFNAM) so that present common usage considers *Pagrus* a synonym of *Sparus*.

The present study, carried out on the Mediterranean and Atlantic species *Sparus aurata*, *Pagrus africanus*, *P. auriga*, *P. caeruleostictus* and *P. pagrus* (all with strong canines anteriorly and two or more rows of molars posteriorly) and based on osteological as well as meristic characters attempts to give a more solid base for the classification of the above species.

MATERIAL EXAMINED

The preserved material was mainly used to collect external morphometric and meristic data and to examine the dentition. Some specimens were also X-rayed. The fresh material was always measured and counted and subsequently skeletonized.

Sparus aurata Linnaeus, 1758

MNHN (Muséum national d'Histoire naturelle, Paris) : total 21 (57 to 485 mm SL). Bassin d'Arcachon (France, Atlantic coast) : 4. Port Etienne (Nouadhibou, Mauritania) : 2. La Rochelle (France, Atlantic coast) : 3. Brest (France, Atlantic coast) : 2. Bay of Biscay : 1. Corse : 1. Nice (France Mediterranean coast) : 1. Naples (Italy) : 1. Alexandria (Egypt, Mediterranean coast) : 1. Thau (France, Mediterranean coast) : 1. Morée (Greece) : 1. Fedala (Mohammedia, Morocco, Atlantic coast) : 1. Timsah (Egypt, Suez Channel) : 1. Lac de Bizerte (Tunisia) : 1.

Fresh material : total 6 (110 to 265 mm SL). Tunis (Tunisia) : 2. Bizerte (Tunisia) : 2. Fiumicino (Italy) : 2.

Pagrus auriga (Valenciennes, 1843)

MNHN : total 10 (110 to 263 mm SL). Port Etienne (Nouadhibou, Mauritania) : 3. Senegal : 5. Algeria : 1. West Africa : 1.

Fresh material : total 2 (227 to 245 mm SL). Bizerte (Tunisia).

Pagrus africanus (Akazaki, 1962)

MNHN : total 11 (180 to 330 mm SL). Senegal : 6. Ivory Coast : 5.

Fresh material : total 8 (162 to 330 mm SL). Guinea-Bissau : 5. Liberia : 3.

Pagrus caeruleostictus (Valenciennes, 1830)

MNHN : total 16 (63 to 470 mm SL): Alexandria (Egypt) : 2. Mauritania : 2. Canary Islands : 1. Senegal : 3. Ivory Coast : 5. Togo : 2. Angola : 1.

Fresh material : total 17 (113 to 350 mm SL). Tunis (Tunisia) : 4. Senegal : 1. Liberia : 11. Ghana : 1.

Pagrus pagrus (Linnaeus, 1758)

MNHN : total 15 (62 to 322 mm SL). Nice (France, Mediterranean coast) : 1. Greece : 2. Naples (Italy) : 1. Madeira : 1. Agadir (Morocco) : 1. Senegal : 6. West Africa : 3.

Fresh material : total 5 (110 to 250 mm SL). Fiumicino (Italy) : 2. Tunis (Tunisia) : 3.

MORPHOLOGY

Colour pattern (in life)

In *Sparus aurata* (Fig. 1) the body is silvery grey, with a black blotch at the origin of the lateral line and a reddish area just below it; there is a yellow golden bar between the eyes, edged by two dark areas. All fins are dusky. The dorsal fin may have a dark band at its midheight; the posterior edge and tips of the caudal fin are black. In *Pagrus auriga* (Fig. 2) the body is pink with four or five dark red, alternatively broad and narrow cross bars which disappear with growth (still well visible at about 25 cm SL). The bands seem to disappear when the sex reversal takes place and the adult females become males. The body of *P. caeruleostictus* (Fig. 3) is pink with characteristic dark blue spots on back and sides, lighter in younger specimens. The dorsal fin has a dark blotch at the base of the last soft rays, the caudal fin is edged with black, males have some yellow and dark green on the head during the reproduction season. The last two species, *P. pagrus* and *P. africanus* (Figs 4 and 5) have a very similar coloration pattern : body pinkish, with silvery reflections with some fine blue spots present especially in young individuals. All fins are pinkish. The only differences between the two species is a dark red blotch at the pectoral fin axils, extending well onto the fin bases, present in *P. africanus* and the white caudal fin tips in *P. pagrus*.

Meristic characters

They are summarized in Table I.

Characters	<i>S. aurata</i> n=21	<i>P. auriga</i> n=9	<i>P. caeruleostictus</i> n=27	<i>P. pagrus</i> n=19	<i>P. africanus</i> n=13
Dorsal spines	11	11	(11) 12	(11) 12	12 (13)
Dorsal rays	12 or 13	10 to 12	(9) 10 (11)	(9) 10	(9) 10
Anal rays	11 (12)	8 (9)	(8) 9	(7) 8	(7) 8
Lat. line scales	73 to 85	50 to 52	51 to 54	50 to 56	46 to 55
Scales between lat.line/ fourth dorsal spine	7 (8)	6 to 6.5	5 or 6	5 or 6 (7)	4 or 5
Total gillrakers on first arch	11 to 13	16 to 19	16 to 20	14 to 17	14 to 17

Osteology

The most interesting osteological differences between *Sparus aurata* and *Pagrus auriga*, *P. caeruleostictus*, *P. pagrus* and *P. africanus* were found in the skull (neurocranium and branchiocranium).



Fig. 1. *Sparus aurata*. (Source: FAO Species Identification Sheets, F.A. 34/47, in part).

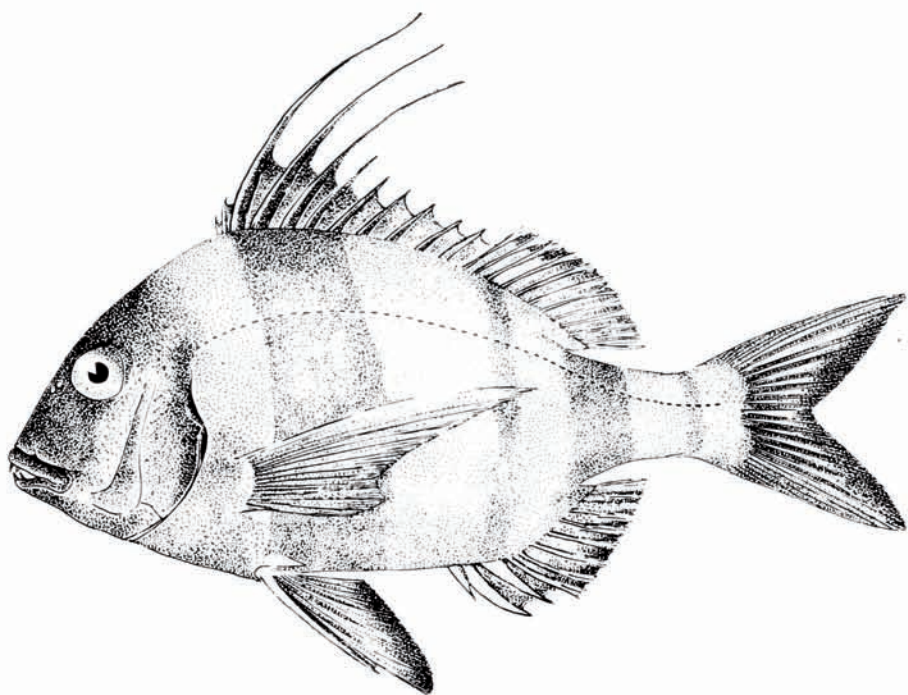


Fig. 2. *Pagrus auriga*. (Source: as in Fig. 1).

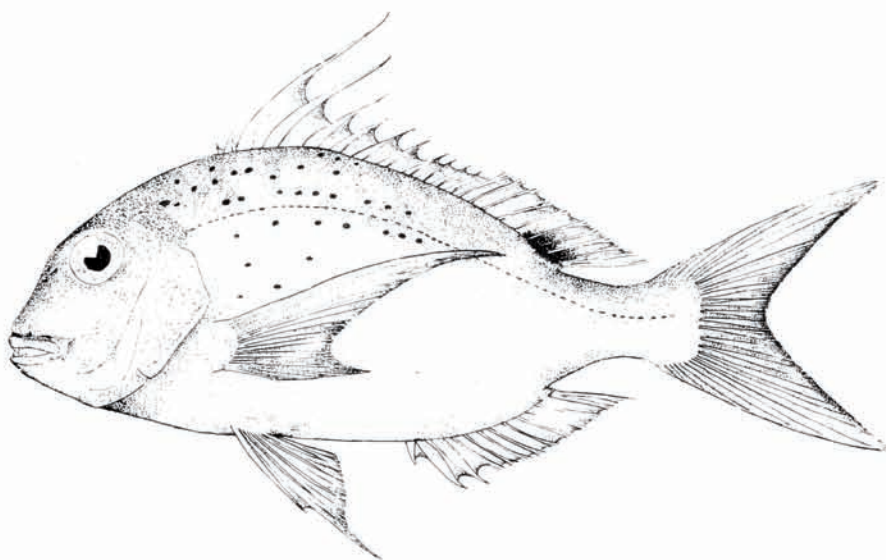


Fig. 3. *Pagrus caeruleostictus*. (Source: as in Fig. 1).

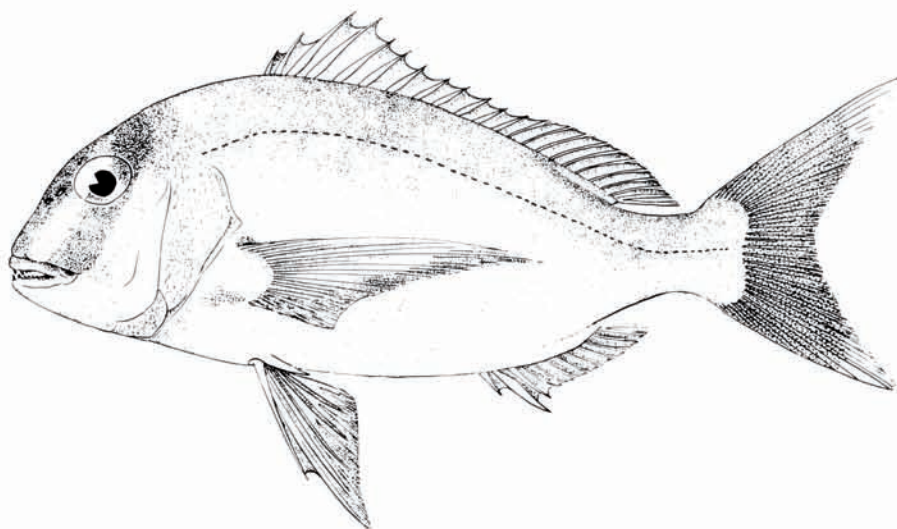


Fig. 4. *Pagrus pagrus*. (Source: as in Fig. 1).

Neurocranium

General description (Figs 6 to 10)

The neurocranium is more elongate in *P. pagrus* and *P. africanus*, less so in *S. aurata*, and quite high in *P. auriga* and *P. caeruleostictus*. In lateral view, its antero-dorsal profile, from the tip of the vomer to the upper posterior tip of the supra-occipital crest, is evenly convex in all the species but *S. aurata* where the upper

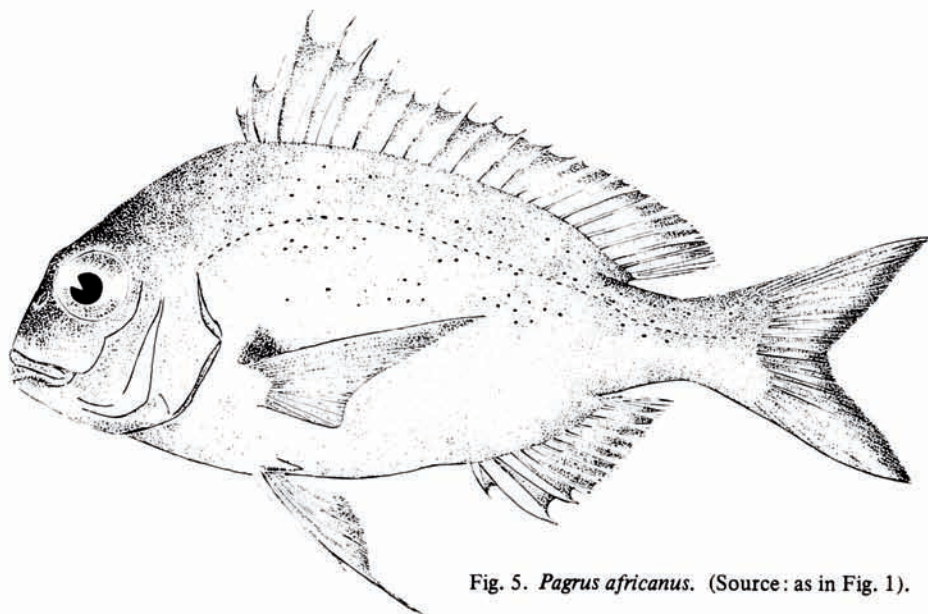


Fig. 5. *Pagrus africanus*. (Source: as in Fig. 1).

surface of the frontals is concave and the antero-dorsal profile irregular. Furthermore, the anterior profile of the ethmoid is equal in length to the anterior profile of the vomer in *S. aurata*, while in the other four species the former is about double the length of the latter. The ventral profile of the skull is formed by the vomer, parasphenoid and basioccipital. The parasphenoid bears a ventral keel, at about its midlength, very pronounced in *P. auriga* and *P. caeruleostictus*, where it is smoothly rounded, and in *S. aurata* where it is pointed, while in *P. pagrus* and *P. africanus* it is moderately pronounced. The posterior profile is formed by the posterior edge of the supraoccipital crest, the exoccipital and the basioccipital. No remarkable differences were noticed in the five species as for the posterior profile.

Two dorso-lateral crests run parallel to the median supraoccipital crest: the inner one originates at the posterior part of the frontal bone, runs on the parietal and terminates at the upper later corner of the epiotic; the outer crest originates at the same point of the inner one and it is formed by the frontal and the pterotic bones.

Ethmoid region

Ethmoid (fig. 11). — The anterior surface is concave in all species, in *S. aurata* it is strongly so and much shorter than in the other species (in lateral view, the anterior profile of the ethmoid is about equal in length to the anterior profile of the vomer in *S. aurata*, it is about double that length in the other species). Two dorso-lateral horns project from the upper margin of the ethmoid.

Lateral ethmoids (sometimes called prefrontals or parethmoids) (Fig. 11). — In *S. aurata*, the median portion bears a large articulating facet for the palatine and

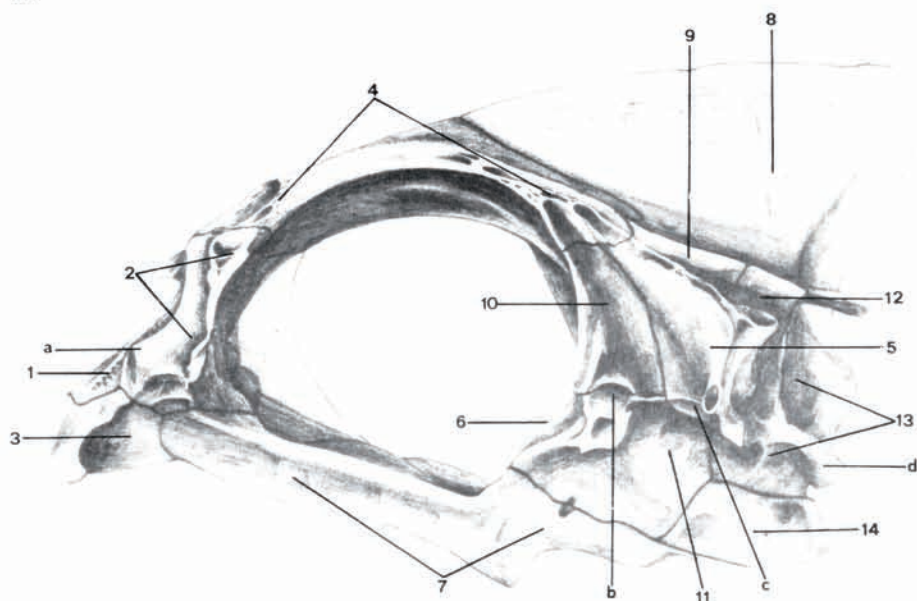


Fig. 6. *P. pagrus* (250 mm SL, Tunisia). Skull (neurocranium), lateral view: 1 ethmoid, 2 lateral ethmoid, 3 vomer, 4 frontal, 5 pterotic, 6 basisphenoid, 7 parasphenoid, 8 supraoccipital crest, 9 parietal, 10 sphenotic, 11 prootic, 12 epiotic, 13 exoccipital, 14 basioccipital. a: articulating facet for palatine; b: articulating facet for anterior condyle of hyomandibula; c: articulating facet for medium condyle of hyomandibula; d: condyle for articulation with first vertebra.

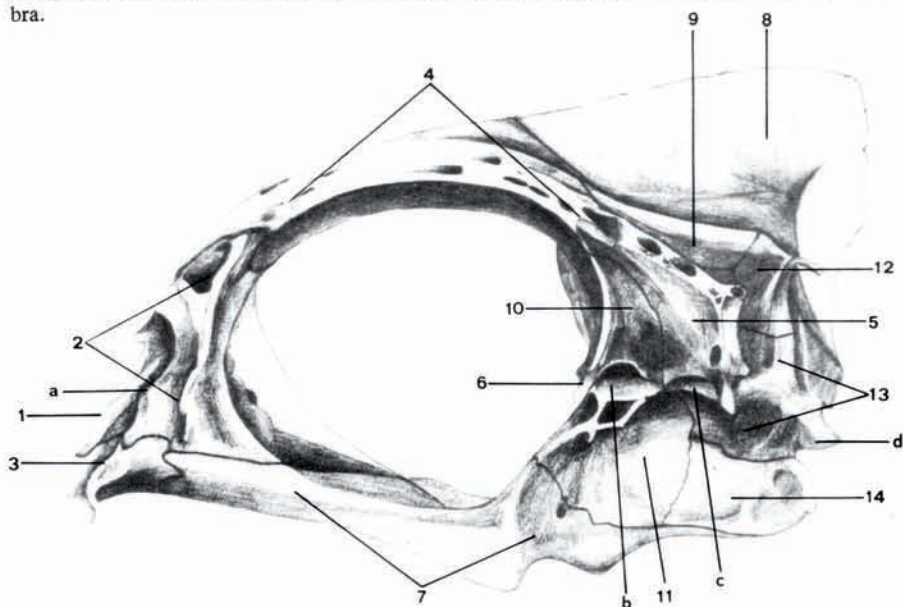


Fig. 7. *P. africanus* (228 mm SL, Guinea Bissau). Skull (neurocranium), lateral view: 1 ethmoid, 2 lateral ethmoid, 3 vomer, 4 frontal, 5 pterotic, 6 basisphenoid, 7 parasphenoid, 8 supraoccipital crest, 9 parietal, 10 sphenotic, 11 prootic, 12 epiotic, 13 exoccipital, 14 basioccipital. a: articulating facet for palatine; b: articulating facet for anterior condyle of hyomandibula; c: articulating facet for medium condyle of hyomandibula; d: condyle for articulation with first vertebra.

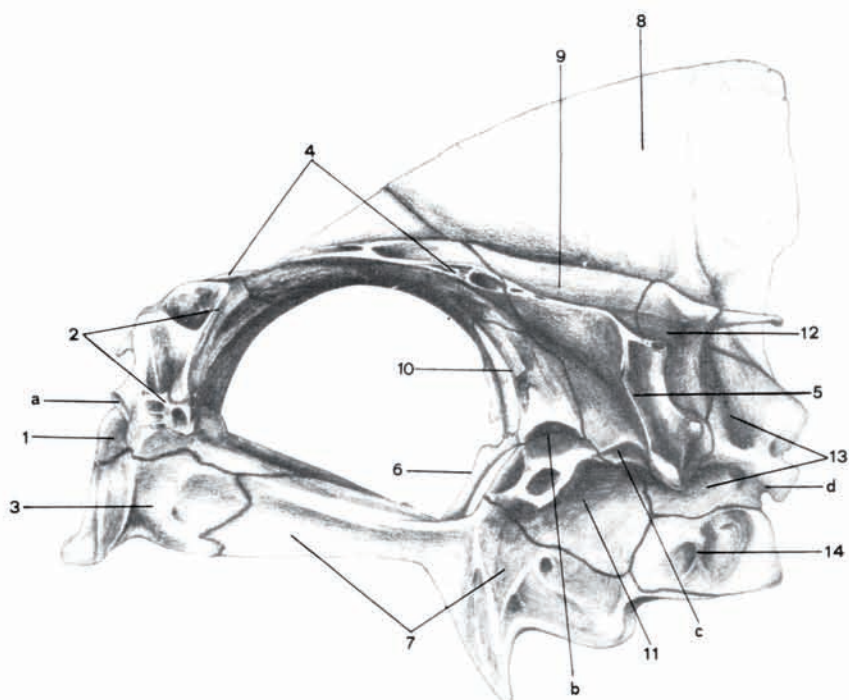


Fig. 8. *S. aurata* (265 mm SL, Tunisia). Skull (neurocranium), lateral view.

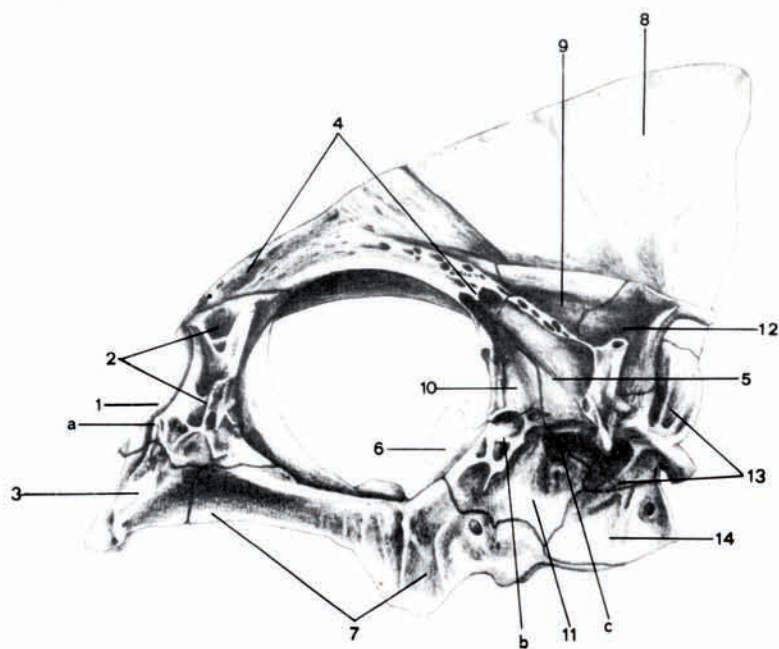


Fig. 9. *P. auriga* (245 mm SL, Tunisia). Skull (neurocranium), lateral view: 1 ethmoid, 2 lateral ethmoid, 3 vomer, 4 frontal, 5 pterotic, 6 basisphenoid, 7 parasphenoid, 8 supraoccipital crest, 9 parietal, 10 sphenotic, 11 prootic, 12 epiotic, 13 exoccipital, 14 basioccipital. a: articulating facet for palatine; b: articulating facet for anterior condyle of hyomandibula; c: articulating facet for medium condyle of hyomandibula; d: condyle for articulation with first vertebra.

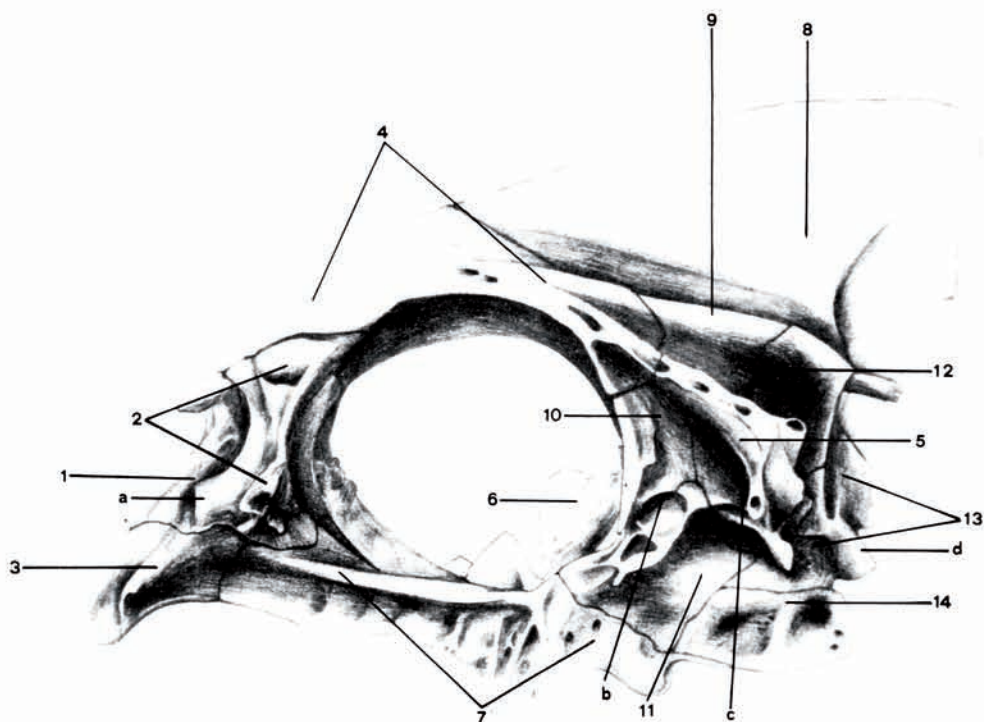


Fig. 10. *P. caeruleostictus* (270 mm SL, West Africa). Skull (neurocranium), lateral view : 1 ethmoid, 2 lateral ethmoid, 3 vomer, 4 frontal, 5 pterotic, 6 basisphenoid, 7 parasphenoid, 8 supraoccipital crest, 9 parietal, 10 sphenotic, 11 prootic, 12 epiotic, 13 exoccipital, 14 basioccipital. a : articulating facet for palatine; b : articulating facet for anterior condyle of hyomandibula; c : articulating facet for medium condyle of hyomandibula; d : condyle for articulation with first vertebra.

an olfactory (orbito-nasal) foramen just above it. The distal portions, forming the lateral wings of the ethmoid region, have an upper, large conical pit (Fig. 11c). In *P. africanus*, *P. auriga*, *M. caeruleostictus* and *P. pagrus* the median and lateral portions of the anterior surface are divided by a ridge which terminates inferiorly just above the articulating facets for the palatines. The olfactory foramen is dorso-medial to the palatine articulating facet (Fig. 11, a, b, d, e).

Vomer (Fig. 11). — It forms the anteriormost part of the cranium. Dorsally it articulates with the ethmoid and the lateral ethmoids; posteriorly, a pointed projection fits into an anterior, conical pocket of the parasphenoid with which it forms the medium axis of the roof of the mouth. In *S. aurata*, the posterior projection has the form of a vertical lamina which articulates, along its posterior edge, with the anterior edge of the ventral lamina of the parasphenoid. The vomer is toothless in all species (family character).

Orbital region, including infraorbital bones.

Frontals. — The frontal articulates anteriorly with the ethmoid and the lateral

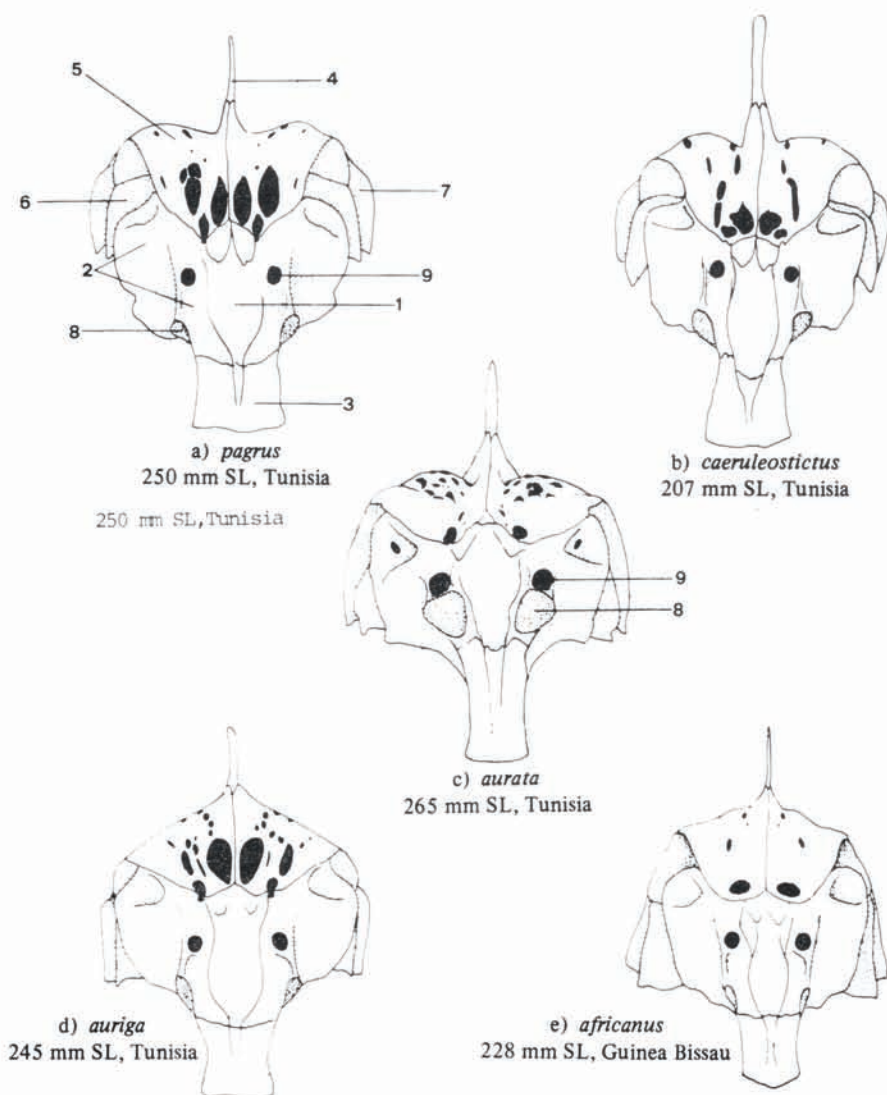


Fig. 11. Skull (neurocranium) anterior view. 1-ethmoid, 2-lateral ethmoid, 3-vomer, 4-supraoccipital crest, 5-frontal, 6-sphenotic, 7-pterotic, 8-articulating facet for palatine, 9-olfactory foramen.

ethmoid, posteriorly with the supraoccipital, pterotic, parietal, sphenotic and pterosphenoïd bones. Posteriorly and laterally, a small lamina joins the sphenotic vertical lamina to form a continuous vertical flange. In *S. aurata* this lamina is missing so that the vertical flange is interrupted. The dorsal surface of the frontal bone is anteriorly convex, rough and porous in *P. auriga*, *P. caeruleostictus*, *P. pagrus* and *P. africanus*, while in *S. aurata* it is concave, with striae running parallel to the interfrontal suture.

Infraorbital bones (1). — The lacrimal is the first bone of the series, forming the anterior part of the maxillary sheath. It is rectangular in shape, deeper than wide, with a projection at the upper anterior corner which is attached to the lateral ethmoid. The upper part of this bone is usually well ossified, the lower half consists of a thin lamina. The shape of this bone does not vary much in the species examined. Only *S. aurata* has the anterior projection more developed (Fig. 12).

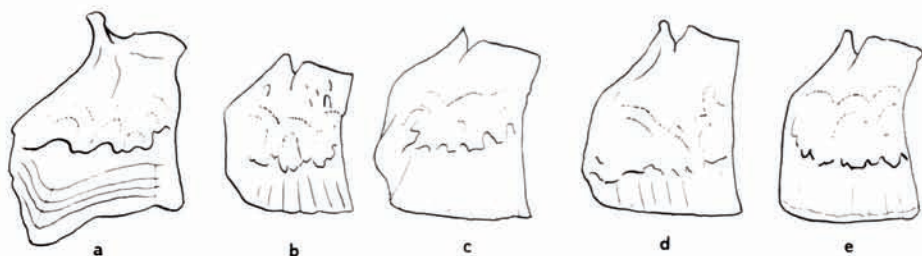


Fig. 12. Lacrimal bones of: a- *aurata* (265 mm SL, Tunisia), b- *africanus* (228 mm SL, Guinea Bissau), c- *pagrus* (250 mm SL, Tunisia), d- *caeruleostictus* (207 mm SL, Tunisia) and e- *auriga* (245 mm SL, Tunisia).

The second suborbital bone forms, together with the first, the lacrimal, a sheath covering the subocular region. It is rectangular in shape, much deeper than wide, its upper part strongly ossified, the lower consisting of a thin lamina. Its upper anterior margin articulates with the posterior edge of the lacrimal. This bone is always as deep as the lacrimal and this is one of the distinguishing characters of the sparoid group (Sparidae, Centracanthidae, Lethrinidae and Nemipteridae) (Akazaki, 1958).

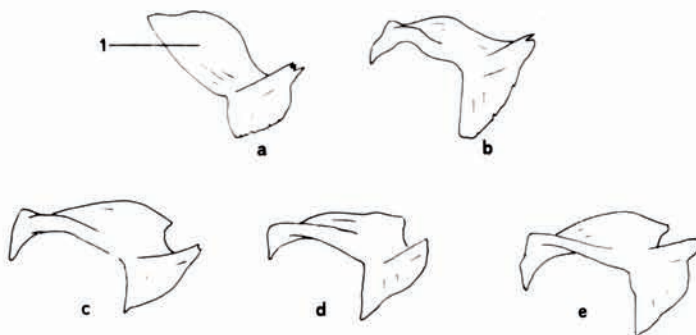


Fig. 13. Third infraorbital of: a- *aurata*, b- *auriga*, c- *pagrus*, d- *africanus* and e- *caeruleostictus*. Length of specimens as in previous figure. 1-subocular shelf.

The third suborbital is composed of a vertical lamina, roughly triangular in shape, with the anterior margin deeper than the posterior one, and the subocular shelf which is attached along the upper margin of the lamina. The subocular shelf is a bony lamina which extends inward and forward to form part of the floor of the orbit. In *P. africanus*, *P. auriga*, *P. caeruleostictus* and *P. pagrus* the subocular shelf is formed by a horizontal lamina, elliptical in shape, ending anteriorly in a triangular, downward directed hook-like, projection (Fig. 13 b to e). In *S. aurata*, only the elliptical lamina is present (Fig. 13a). Smith and Bailey (1962) suggested that one of the possible functional significances of the subocular shelf is to strengthen the entire complex of structures in the subocular area.

Branchiocranium

Mandibular arch

It is composed of the upper jaw (premaxilla and maxilla) and the lower jaw (dentary, angular and retroarticular). The premaxilla and dentary bear teeth.

Dentition. — Two types of teeth characterize these species : molars and canines; blunter canines are also present as intermediates. The number of rows of molars in the lower jaw has been used by Cuvier to separate this group of fishes into two genera, *Sparus* and *Pagrus*, the former characterized by having two to four rows, the latter two or three. However, since the number of rows increases with size, it has been considered insufficient for the separation of the group into two genera and all the species have been finally grouped under the genus *Sparus* (Linnaeus, 1758 ; Tortonese, 1970). In *S. aurata* four to six strong canines are present in front of each jaw (usually six), followed by two to four rows of molars. The number of rows of teeth seems to vary according to the size of the individuals : at about 50 mm (Fig. 14-1) there are two or three rows, the outer row consisting of

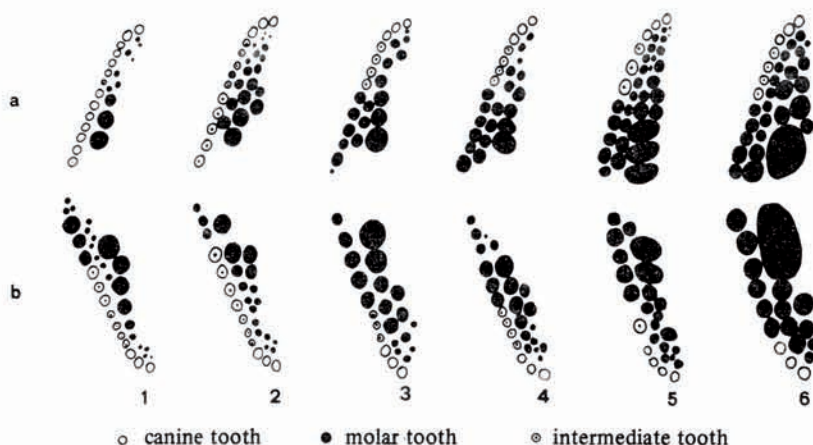


Fig. 14. *S. aurata* : teeth in right half of upper jaw (a) and lower jaw (b) in specimens of different size : 1) 46 mm SL (Bay of Biscay). 2) 74 mm SL (La Rochelle, France). 3) 87 mm SL (Bassin d'Arcachon, France). 4) 98 mm SL (Bassin d'Arcachon, France). 5) 206 mm SL (Bassin d'Arcachon, France). 6) 280 mm SL (Morée, France).

teeth not yet molar-like, but intermediate in shape between the canines and the molars. At about 150 mm most of these teeth have become real molars and usually four rows are visible in the upper and three in the lower jaw, the third row with 1 or 2 very enlarged teeth posteriorly in each jaw. From a size of about 200 mm (Fig. 14-5), two extremely large molar teeth appear posteriorly in each jaw and can be observed in *S. aurata* only. In the other species (Figs 15 to 18) there are usually four canines in upper and six in lower jaw, followed by blunter teeth which become progressively molariform posteriorly arranged in two or three rows. Small teeth are also present just behind the canines in all species. In *S. aurata* and *P. caeruleostictus* however, these small teeth are granular, in the other species they have pointed tips and in *P. pagrus* they are particularly numerous.

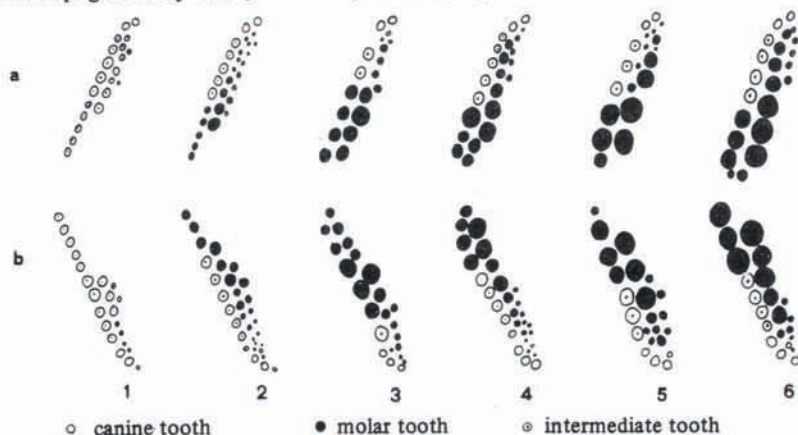


Fig. 15. *P. caeruleostictus* : teeth in right half of upper jaw (a) and lower jaw (b) in specimens of different size : 1) 63 mm SL (Alexandria, Egypt). 2) 88 mm SL (Alexandria, Egypt). 3) 160 mm SL (Mauritania). 4) 190 mm SL (Togo). 5) 235 mm SL (Senegal). 6) 380 mm SL (Ivory Coast).

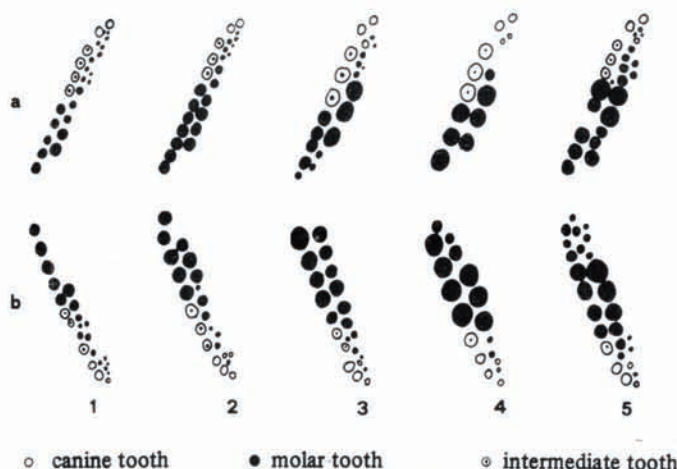


Fig. 16. *P. auriga* : teeth in right half of upper jaw (a) and lower jaw (b) in specimens of different size : 1) 110 mm SL (Nigeria). 2) 142 mm SL (Mauritania). 3) 187 mm SL (Mauritania). 4) 215 mm SL (Mauritania). 5) 255 mm SL (West Coast of Africa).

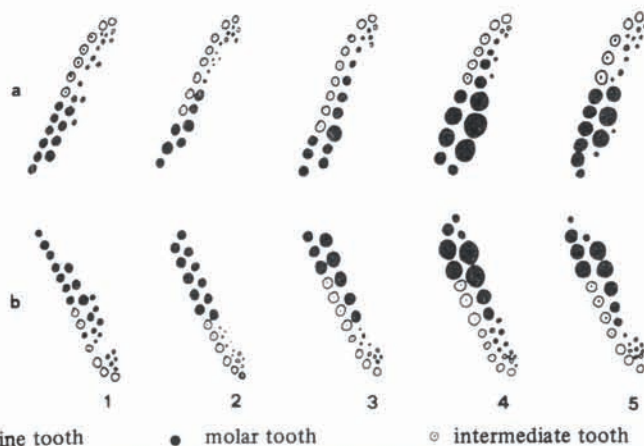


Fig. 17. *P. pagrus* : teeth in right half of upper jaw (a) and of lower jaw (b) in specimens of different size : 1) 82 mm SL (Greece). 2) 122 mm SL (Greece). 3) 175 mm SL (Senegal). 4) 269 mm SL (Morée, France). 5) 305 mm SL (Nice, France).

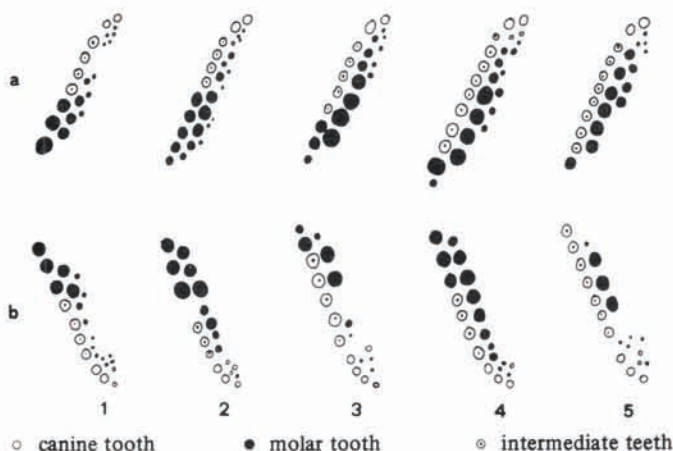


Fig. 18. *P. africanus* : teeth in right half of upper jaw (a) and of lower (b) in specimens of different size : 1) 131 mm SL (Ivory Coast). 2) 180 mm SL (Dakar, Senegal). 3) 240 mm SL (West Coast of Africa). 4) 280 mm SL (West Coast of Africa). 5) 330 mm SL (Ivory Coast).

Premaxilla (Fig. 19). — It is composed of a horizontal ramus bearing teeth and a vertical peticel, the latter usually shorter than or as long as the former; in *P. africanus*, the peticel is considerably shorter than the ramus. In all species the ramus is stout, particularly so in *S. aurata*, because of the large number of molars and the presence of one (in individuals longer than about 150 mm SL) very large teeth posteriorly on each side. The anterior canines are particularly long and forward projecting in *P. auriga*. The posterior tip of the premaxilla ramus overlaps the maxilla (1).

(1) Family feature, also shared by the family Centracanthidae, but missing in the other sparoid family Nemipteridae and Lethrinidae (Johnson, 1981).

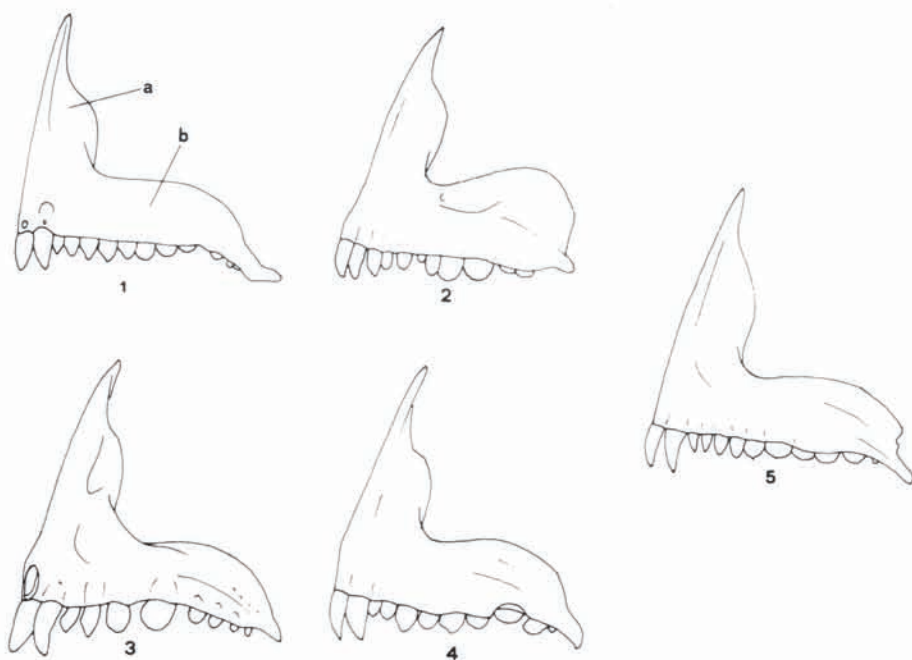


Fig. 19. Lateral view of left premaxilla of : 1) *africanus* (228 mm SL, Guinea Bissau), 2) *aurata* (165 mm SL, Tunisia), 3) *auriga* (245 mm SL, Tunisia), 4) *caeruleostictus* (207 mm SL, Tunisia), 5) *pagrus* (250 mm SL, Tunisia). a = peticel. b = ramus.

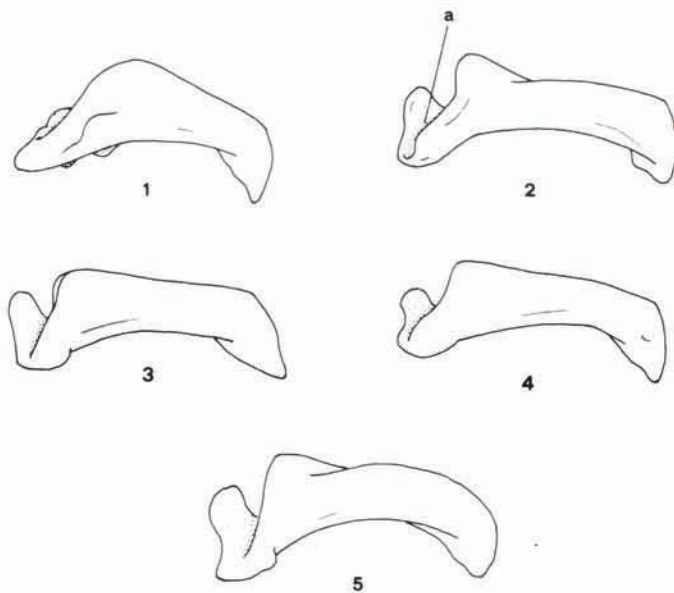


Fig. 20. Lateral view of left maxilla of : 1) *aurata* (165 mm SL, Tunisia), 2) *auriga* (245 mm SL, Tunisia), 3) *africanus* (228 mm SL, Guinea Bissau), 4) *caeruleostictus* (207 mm SL, Tunisia), 5) *pagrus* (250 mm SL, Tunisia). a = groove for the articulation with the palatine.

Maxilla (Fig. 20). — It is almost completely concealed by the subocular sheath and lies along the upper half of the premaxilla ramus, posteriorly extending beyond it. It is formed by an outer lamina and an inner upper and inner lower projections, anteriorly located, forming respectively a groove for the articulation with the palatine and one for the premaxilla. These processes are quite strong in all species, but they are weaker in *S. aurata*. Also the shape of the outer lamina, in lateral view, looks quite different in *S. aurata*, being deeper near midlength instead of anteriorly. The anterior margin of the outer lamina is more concave in *P. auriga* than in the other species where it is almost straight.

Dentary (Fig. 21). — It is formed by an upper, horizontal dentigerous branch and an oblique ventral branch. At the corner formed by the two branches a pocket fits the triangular anterior projection of the angular. In *P. auriga*, the ventral branch is much shorter than the upper one, while in the other species they are of about the same length, and the symphysis is longer, being more than half the length of the anterior margin. The dentary appears to be massive in *S. aurata*, for having more rows of teeth and a very large posterior tooth (in specimens more than about 200 mm long).

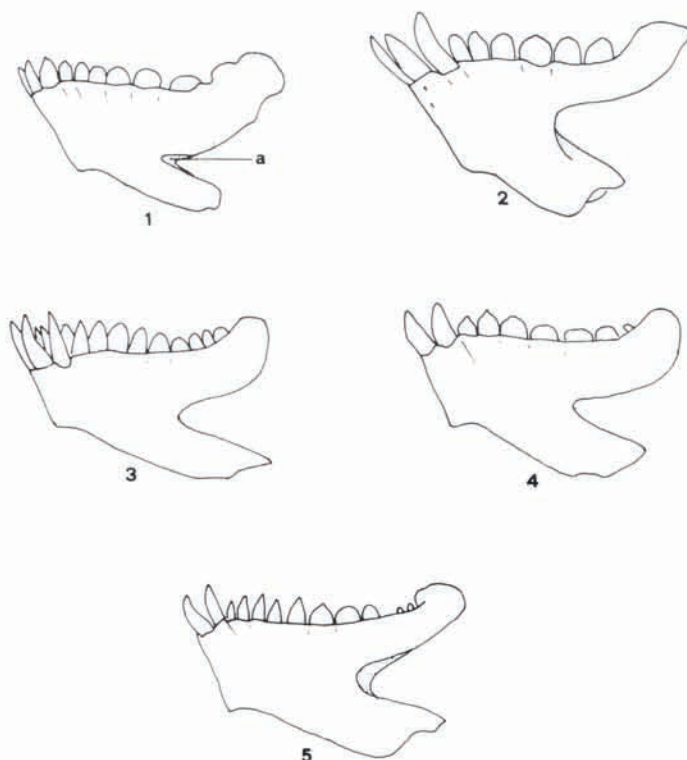


Fig. 21. Lateral view of left dentary of : 1) *aurata*, 2) *auriga*, 3) *africanus*, 4) *caeruleostictus*, 5) *pagrus* (length and provenance of fish as in preceding figure). a = pocket for the articulation with angular.

Palatine arch (Fig. 28)

It forms the roof of the mouth and consists of four pairs of bones: palatine, ectopterygoid, endopterygoid and metapterygoid. It is attached to the hyoid arch through articulations with the hyomandibula, the quadrate and symplectic.

Palatine (Fig. 22). — This bone is connected to the maxilla by means of an anteriorly directed projection which fits into a corresponding groove of the maxilla; with the lateral ethmoid, by means of an articulating facet located at mid-length of its upper margin; with the ectopterygoid and endopterygoid along its posterior margin. The shape of this bone seems to be rather constant in the species under study. Only in *S. aurata* it appears to be stouter, with a strong anterior projection and a shorter lower process. Also, the facet which articulates with the lateral ethmoid is larger in *S. aurata*.

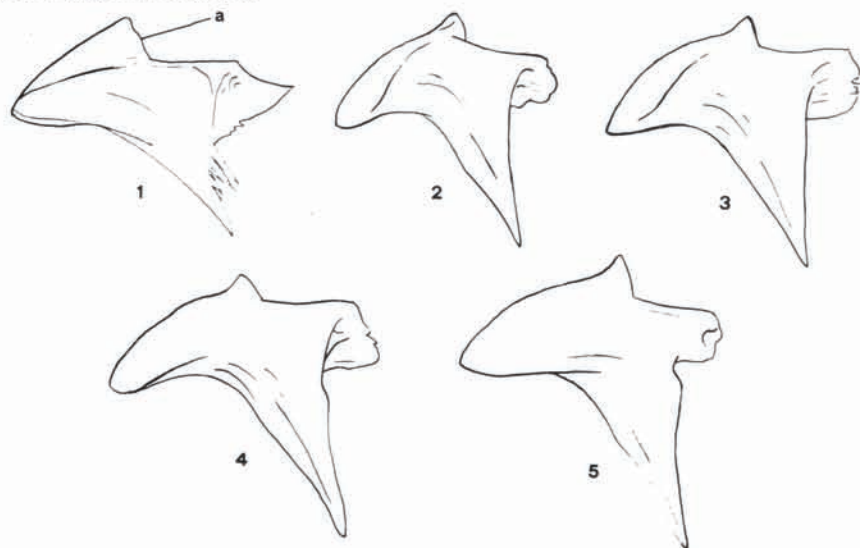


Fig. 22. Lateral view of left palatine of: 1) *aurata*, 2) *africanus*, 3) *auriga*, 4) *caeruleostictus*, 5) *pagrus* (length and provenance of fish as in Fig. 20). a = position of articulating facet for lateral ethmoid.

Ectopterygoid (Fig. 23). — It is an elongate bone which, in *S. aurata*, articulates dorsally with the palatine and along its posterior margin with the endopterygoid, by which it is partially covered, and the quadrate. In the other species, the upper anterior part of this bone is covered by the palatine (Fig. 28).

Endopterygoid (Fig. 24). — Also in this case, remarkable differences in the shape can be found between *S. aurata* and the other four species as shown in Figure 24. The endopterygoid articulates anteriorly with the palatine and the ectopterygoid, posteriorly with the metapterygoid and inferiorly with the quadrate. In *S. aurata* there is almost no overlapping between this bone and the metapterygoid while, in the other species, the posterior part of the endopterygoid is overlapped by the metapterygoid (Fig. 28).

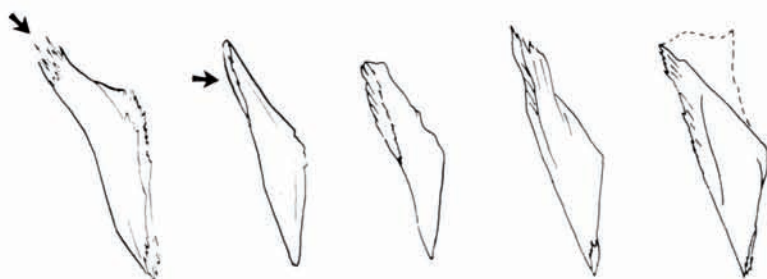


Fig. 23. Lateral view of left ectopterygoid of : 1) *aurata*, 2) *africanus*, 3) *auriga*, 4) *caeruleostictus*, 5) *pagrus* (length and provenance of fish as in Fig. 20). Arrow indicates point of attachment of palatine.

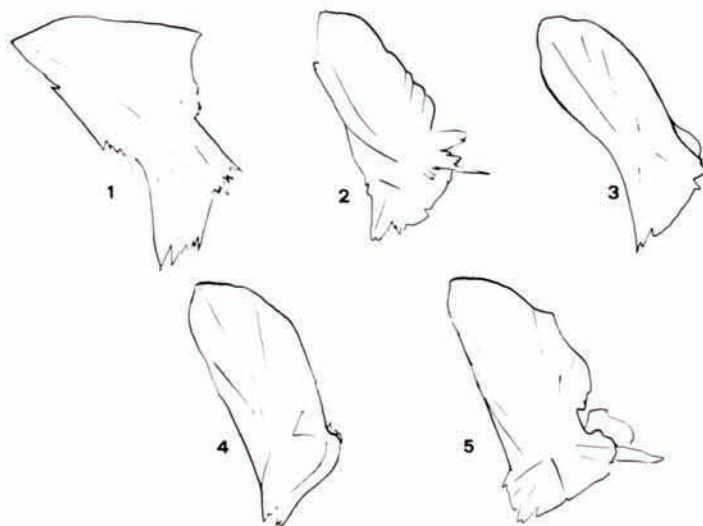


Fig. 24. Lateral view of left endopterygoid of : 1) *aurata*, 2) *africanus*, 3) *auriga*, 4) *caeruleostictus*, 5) *pagrus* (length and provenance of fish as in Fig. 20).

Metapterygoid (Fig. 25). — It is more or less rectangular in shape. It articulates anteriorly with the endopterygoid, posteriorly with the hyomandibula, and ventrally with the quadrate and the symplectic, which overlaps its lower posterior corner. In *S. aurata* the anterior margin is deeply emarginate, forming an obtuse angle which fits the corresponding angle of the posterior margin of the endopterygoid. According to Johnson (1980), one of the distinctive characters of the sparoid suspensorium is the « direct osseous articulation at all junctions except that between the quadrate and the metapterygoid ». However, in *S. aurata*, an ossified projection at the antero-ventral corner of the metapterygoid articulates with the quadrate (Fig. 27, 1).

Hyoid arch

It is a chain of bones which connects the lower jaw, the roof of the mouth

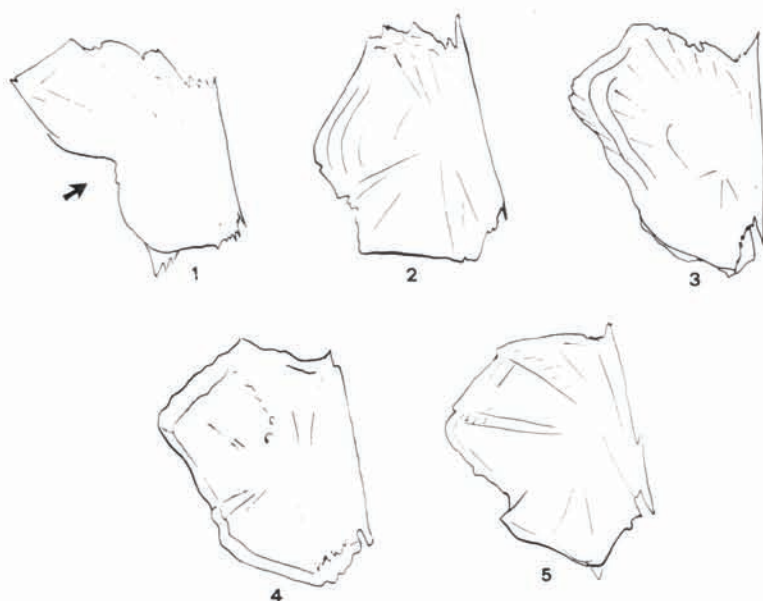


Fig. 25. Lateral view of left metapterygoid of : 1) *aurata*, 2) *africanus*, 3) *auriga*, 4) *caeruleostictus*, 5) *pagrus* (length and provenance of fish as in Fig. 20). Arrow indicates obtuse angle with in *aurata* corresponds to the articulation with the ectopterygoid.

and the opercular apparatus with the skull. It is composed of: hyomandibula, quadrate, symplectic, interhyal, epihyal, ceratohyal and the unpaired glossohyal.

Hyomandibula (Fig. 26). — It suspends the operculum, the lower jaw, the palatine arch, and the remaining bones of the hyoid complex to the neurocranium. It is formed by a massive part dorsally, a vertical shaft and an anterior lamina attached along the upper anterior margin of the shaft. The dorsal part bears three condyles: the anterior one fits into the fossa formed by the sphenotic and prootic bones, the median one fits in the pterotic fossa and the posterior one is attached to the inside of the opercle. The posterior condyle is ventrally directed in *S. aurata* and *P. auriga*, horizontally directed in the remaining species. The shaft is dorsally continuous with a projection which is longer and extends beyond the median condyle in *S. aurata*, it is shorter and does not extend beyond the median condyle in *P. africanus*, *P. auriga*, *P. caeruleostictus* and *P. pagrus*. Posteriorly, it has a long articulation with the preopercle, anteriorly with the metapterygoid (Fig. 28). The species can be divided into three groups according to the shape of the lamina and of the outer ridge: *S. aurata*, *P. auriga* and *P. caeruleostictus*, *P. pagrus* and *P. africanus*.

Quadrate (Fig. 27). — The shape of this bone is quite similar in all species except *S. aurata* where the posterior portion is prolonged into a dorsal process. The quadrate articulates dorsally with the endopterygoid, by overlapping it, the metapterygoid and the symplectic, the lower part of which fits into a groove on its inner surface; anteriorly, it articulates with the ectopterygoid and, by means of a large

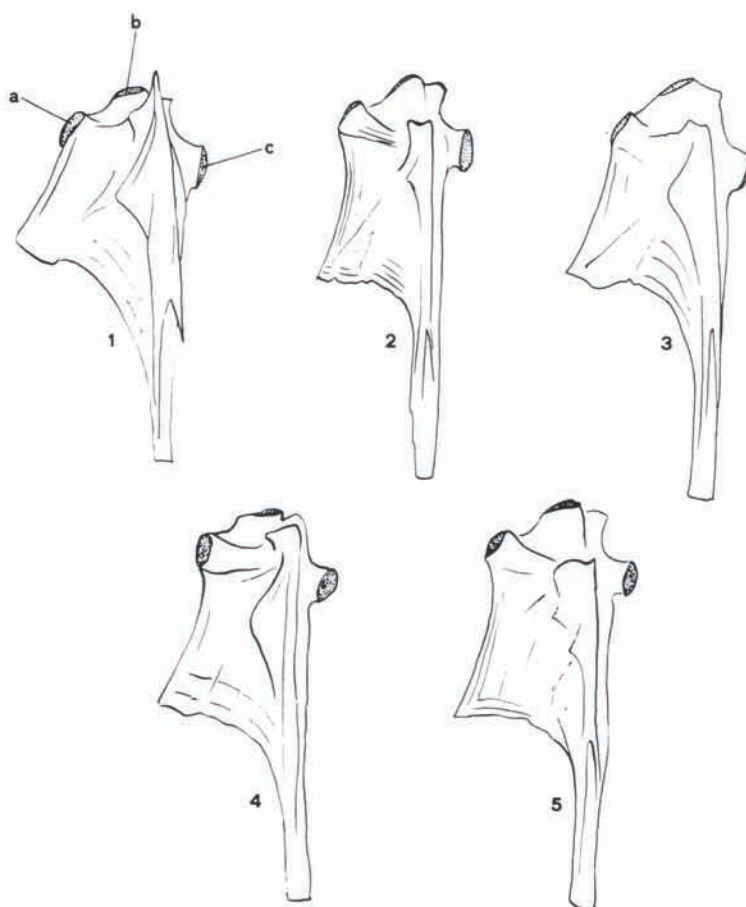


Fig. 26. Lateral view of left hyomandibula of : 1) *aurata*, 2) *africanus*, 3) *auriga*, 4) *caeruleostictus*, 5) *pagrus* (length and provenance of fish as in Fig. 20). a = anterior condyle for articulation with fossa at sphenotic-ptotic junction. b = medium condyle for articulation with pterotic fossa. c = posterior condyle for articulation with opercle.

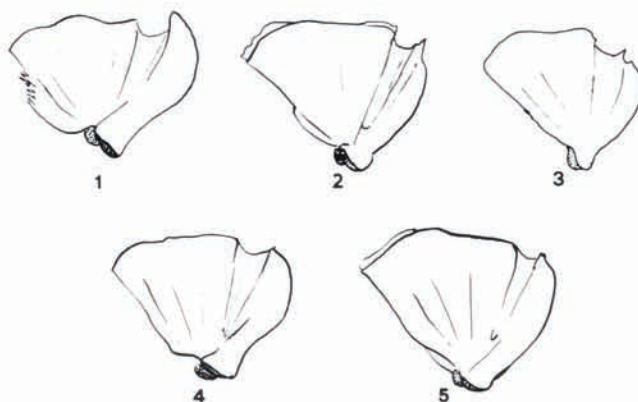


Fig. 27. Lateral view of left quadrate. 1) *aurata*, 2) *africanus*, 3) *auriga*, 4) *caeruleostictus*, 5) *pagrus*. (Length and provenance of fish as in Fig. 20).

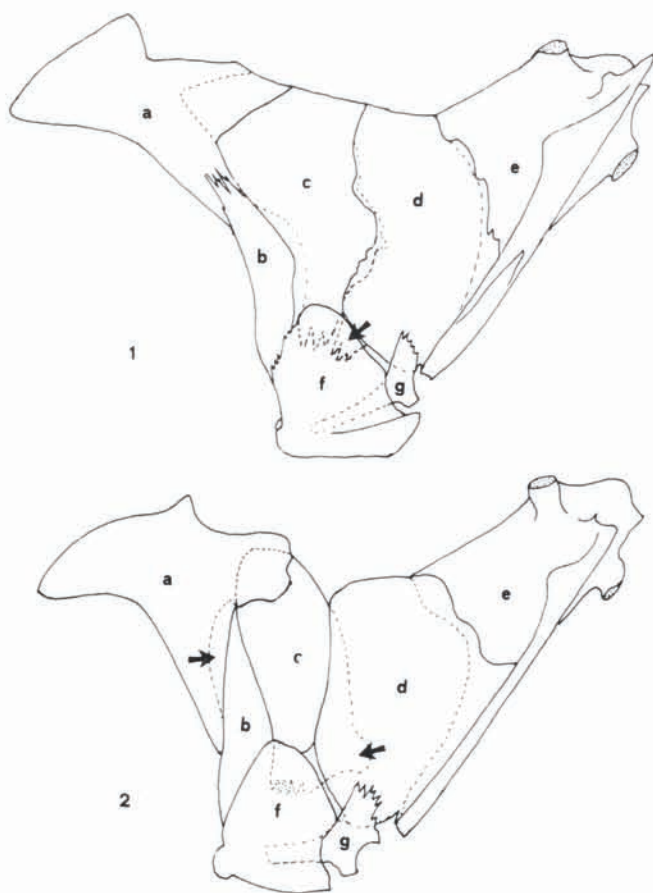


Fig. 28. Lateral view of part of left suspensorium : 1) *aurata* (265 mm SL, Tunisia) and 2) schematic for *africanus*, *auriga*, *caeruleostictus* and *pagrus*. Arrows indicate overlapping areas which differ in the two groups. a = palatine. b = ectopterygoid. c = endopterygoid. d = metapterygoid. e = hyomandibula. f = quadrate. g = symplectic.

articulating facet, with the angular (Fig. 28). The upper anterior margin of the subopercle is attached to the lower margin of the quadrate.

Urohyal (Fig. 29). — The urohyal is more or less triangular in shape, with a thick lower margin articulating anteriorly with the hypohyals of both sides. In *S. aurata* the antero-dorsal margin is thickened and bears a dorsally directed projection anteriorly; the lower margin ends posteriorly with two strong branches forming a V. In *P. auriga* the anterior margin is also thickened and there is only a very small, spine-like dorsally-directed projection; the lower margin ends in a small bifurcation, more evident in older specimens. In *P. caeruleostictus*, *P. pagrus* and *P. africanus* the anterior margin is not thickened, it bears a very small spine in the former one and it is smooth in the latter two. In these species the thickened lower margin ends in a very small V, more or less visible according to age.

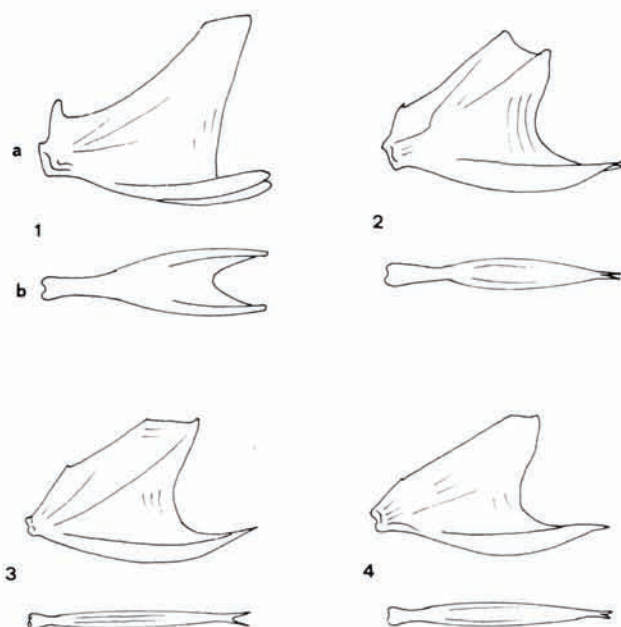


Fig. 29. Lateral view (a) and ventral view (b) of the urohyal in 1) *aurata*, 2) *auriga*, 3) *caeruleostictus*, 4) *pagrus* (a length and provenance of fish as in Fig. 20).

CONCLUSIONS

Table II summarizes the most important differentiating characters between the species under study.

Several meristic as well as osteological characters separate *S. aurata* from the other species. The most interesting differences are, among the meristic characters: the number of dorsal soft rays (12 or 13 against a range of 10 to 12 in the other species); the number of anal rays (more numerous, 11 against 8); the number of lateral-line scales (73 to 85 against 46 to 56) the number of gill rakers on first arch (fewer in *S. aurata* 11 to 13, against the 16 to 19 in *P. auriga* and *P. caeruleostictus* and 14 to 17 in *P. pagrus* and *P. africanus*); among the osteological characters: the articulating facet for the palatine (much larger in *S. aurata* than in the other species), the articulation between the vomer and the parasphenoid, the absence, in *S. aurata*, of a posterolateral lamina on the frontal, the shape of the dorsal surface of the frontal (concave in *S. aurata*, convex in the other species), the shape of the subocular shelf, which is not «hooked» in *S. aurata* only, the articulation ectopterygoid/endopterygoid (non overlapping in *S. aurata*), the direct articulation between the metapterygoid and the quadrate (present in *S. aurata* only) and the shape of the glossohyal, which in *S. aurata* has a very thick lower margin, posteriorly ending in a very strong V.

Although the phylogeny of these species will be better understood only when the interrelationships between the related groups (e.g. other genera within the fami-

ly and related families) will be clarified, the genus *Sparus* (*sensu lato*) is already clear and we propose that the original separation of *Pagrus* from *Sparus*, as adopted by the majority of the authors after Cuvier established the genus *Pagrus*, be maintained. We agree with Munro (1949) in considering *Sparus* a monotypic genus which should include *S. aurata* only. The genus *Pagrus* should include *P. auriga*, *P. caeruleostictus*, *P. pagrus* and *P. africanus*.

Table II

Characters	<i>S. aurata</i>	<i>P. auriga</i>	<i>P. caeruleostictus</i>	<i>P. pagrus</i>	<i>P. africanus</i>
Dorsal spines	11	11	(11) 12	(11) 12	12 (13)
Dorsal rays	12 or 13	10 to 12	(9) 10 (11)	(9) 10	(9) 10
Anal rays	11 (12)	8 (9)	(8) 9	(7) 8	(7) 8
Lat. line scales	73 to 85	50 to 52	51 to 54	50 to 56	46 to 55
Scales between lat. line and fourth dorsal spine	7 (8)	6 to 6.5	5 or 6	5 or 6 (7)	4 or 5
Total gillrakers on first arch	11 to 13	16 to 19	16 to 20	14 to 17	14 to 17
Preopercular scalation	absent	present	present or absent	absent	absent
Articulating facet for palatine on lateral ethmoid	very large	medium	medium	medium	medium
Anterior projection of parasphenoid for articulation with vomer	a lamina	a cone (fitting a conical posterior projection of the vomer)	a cone	a cone	a cone
Posterolateral lamina of frontal	absent	present	present	present	present
Dorsal surface of frontal	concave	convex	convex	convex	convex
Parasphenoid ventral keel	strong and pointed	strong and rounded	strong and rounded	weak	weak
Subocular-shelf anterior "hook"	absent	present	present	present	present
Rows of molars (adults beyond 15 cm)	3 or 4	2 or 3	2 or 3	2 or 3	2 or 3
Dentary ventral branch	as long as dentigerous branch	much shorter than dentigerous branch	as long as dentigerous branch	as long as dentigerous branch	as long as dentigerous branch
Endopterygoid/ectopterygoid articulation	almost no overlapping	posterior part of endopterygoid overlapping metapterygoid	posterior part of endopterygoid overlapping metapterygoid	posterior part of endopterygoid overlapping metapterygoid	posterior part of endopterygoid overlapping metapterygoid
Glossohyal ventral keel	present	absent	absent	absent	absent
Articulation metapterygoid/quadrate	through an antero-ventral projection of the metapterygoid	no direct osseous articulation	no direct osseous articulation	no direct osseous articulation	no direct osseous articulation
Urohyal ventral margin	with a very strong bifurcation	bifurcation very weak or absent	bifurcation very weak or absent	bifurcation very weak or absent	bifurcation very weak or absent

Acknowledgements. I wish to thank Dr M.L. Bauchot (MNHN, Paris) for permission to examine specimens and her willingness to discuss problems, Dr W. Fischer (FAO, Rome) for his support and encouragement, and Dr B.B. Collette (NMFS Systematics Laboratory, Washington) for his useful comments.

REFERENCES

- AKAZAKI, M., 1958. — Studies on the orbital bones of Sparoid fishes. *Zool. Mag., Tokyo*, 67 : 322-25, 1 fig. (English summary).
- 1962. — Studies on the spariform fishes. Anatomy, phylogeny, ecology and taxonomy. Misaki Marine Biological Institute, Kyoto University, Special Report, No. 1, 68 pp.
- BERTIN, L., 1958. — Squelette appendiculaire. *In* Traité de Zoologie. Masson et Cie, Paris, 13 (1) : 710-47 (P.P. Grassé, ed.).
- BINI, G., 1968. — Atlante dei pesci delle coste italiane. Mondo sommerso, Milano, IV.
- CUVIER, G., 1817. — Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Nouvelle édition, Paris, 1 : 272.
- DAGET, J., 1964. — Le crâne des téléostéens. *Mém. Mus. Nat. Hist. Nat., Série A, Zoologie* XXXI (2) : 163-340.
- FISCHER, W., G. BIANCHI & W.B. SCOTT (eds), 1981. — FAO species identification sheets for fishery purposes. Eastern Central Atlantic; fishing areas 34,47 (in part). Canada Funds-in-Trust. Ottawa, Department of Fisheries and Oceans, Canada, by arrangement with the Food and Agriculture Organization of the United Nations, 1-7 : pag. var.
- FOWLER, H.W., 1933. — The fishes of the families Banjosidae, Lethrinidae, Sparidae, Enoplosidae collected by the United States Bureau of Fisheries Steamer ALBATROSS chiefly in the Philippine Seas and adjacent waters. *Bull. U.S. natn. Mus.*, 100 (12) : 138-81.
- GOSLINE, W.A., 1961. — The perciform caudal skeleton. *Copeia* 1961 (3) : 265-70.
- HUREAU J.C. & T.H. MONOD (eds), 1973. — Check-list of the Fishes of the North-eastern Atlantic and of the Mediterranean (CLOFNAM), Unesco, Paris, 405-15.
- JOHNSON, G.D., 1975. — The procurrent spur; an undescribed perciform caudal character and its phylogenetic implications. *Occas. Pap. Calif. Acad. Sci.*, 121, 23 p.
- 1981. — The limits and relationships of the Lutjanidae and associated families. Univ. Calif. Press. Bulletin of the Scripps Institution of Ocean., University of California, 24.
- JORDAN, D.S. & B.W. EVERMANN, 1896-1900. — The Fishes of North and Middle America, a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the isthmus of Panama. *Bull. U.S. natn. Mus.*, (47), Part II, 1898 : 1343-64.
- JORDAN, D.S. & B. FESLER, 1893. — A review of the Sparoid Fishes of America and Europe. *Rep. U.S. Commnr. Fish.* for 1889-91, 17 : 421-544, 55 pl.
- JORDAN, D.S. & W.F. THOMPSON, 1914. — Record of the fishes obtained in Japan in 1911. *Mem. Carneg. Mus.*, 6 : 205-313.
- LINNAEUS, C. 1758. — *Systema Naturae*, ed. X. 1, 824 p. Nantes & Pisces : 277 (reprint, 1956, London).
- MUNRO, I.S.R., 1949. — Revision of Australian silver breams *Mylio* and *Rhabdosargus*. *Mem. Queensland Museum*, XII (4).
- NELSON, G.J., 1969. — Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bull. Am. Mus. Nat. Hist.*, 141 : 4, 477-552.
- REGAN, C.T., 1913. — Classification of the Percoid fishes. *Ann. Mag. Nat. Hist.*, 8, 12 : 111-45.

- SMITH, J.L.B., 1938. — Sparidae and Denticidae. *Trans. Roy. Soc. S.A.*, XXVI : 255.
- SMITH, C.L. & R.M. BAILEY, 1962. — The subocular shelf of fishes. *J. Morphol.*, 110 (1) : 1-17.
- TOMIYAMA, I., 1931. — Comparative studies on the opisthotic bone of Sparidae. *J.Fac. Sci., Imp. Univ. Tokyo*, Sect. 4 : 2 (4) : 309-17.
- TORTONESE, E., 1970. — Osteichthyes (Pesci ossei), Parte Prima. Fauna ital. 10. Calderini, Bologna, 565 p., 198 fig.
- YASUDA F. & K. MIZUGUCHI, 1969. — A study on the osteological characters of six Sparid fishes referred to the genera *Chrysophrys* and *Pagrus*. *Jap. Journ. Ichth.*, 16 (1) : 31-34, fig 1.